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The larval development of palaemonid shrimps from the Amazon Region reared in the laboratory. VI. Abbreviated development of *Macrobrachium nattereri* (HELLER, 1862) (Crustacea: Decapoda)

by

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Abstract

The larval development of the freshwater shrimp *Macrobrachium nattereri* (HELLER) was studied in the laboratory based on the offspring of a berried female collected in a small, terra-firme, forest stream near Manaus. Larval development was abbreviated, with 3 larval stages. Yolk-rich larvae subsisted, without feeding, until metamorphosis and were benthic. The newly-hatched larva had sessile eyes and all appendages, except for the uropods; however, most of the appendages were not fully formed. Larval period did not exceed 8 days. Descriptions and illustrations of the 3 larval and first juvenile stages are presented. Comparisons are made with the larvae of other known South American *Macrobrachium* species with abbreviated larval development.

Keywords: **Crustacea, Palaemonidae, *Macrobrachium nattereri*, larval development, Amazon Region.**

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Introduction

Recent studies have increased our knowledge on the abbreviated larval development of some palaemonids shrimps. In Asia, several species of *Macrobrachium* are known to show abbreviated development (see SHOKITA 1977 and CHONG & KHOO 1987a, b for further references). In the Amazon Region, many species of palaemonids have abbreviated, or even extremely abbreviated larval development (MAGALHÃES 1986; 1986/87; MAGALHÃES 1988; MAGALHÃES & WALKER 1988). Brief comparative descriptions of the first larval stage of several Amazonian palaemonids, including *M. nattereri,* was presented by MAGALHÃES & WALKER (1988). Other South American species of *Macrobrachium* for which this type of development has been fully described are *M. potiuna* (MÜLLER) (cf. MÜLLER 1892; BUENO unpubl.), *M. jelskii* (MIERS) (cf. GAMBA 1980), *M. iheringi* (ORTMANN) (cf. BUENO unpubl.) and *M. brasiliense* (HELLER) (cf. VEGA unpubl.).

CHONG & KHOO (1987b) discussed the potential use of larval characters as taxonomic tools in species identification and classification. HOLTHUIS (1952) and KENSLEY & WALKER (1982) mention the difficulties of taxonomic studies of the genus *Macrobrachium.* Such difficulties may be encountered by one studing this group in the Central Amazonian Region where at least four closely related species of *Macrobrachium* occur: *M. nattereri, M. brasiliense, M. ferreirai* KENSLEY & WALKER and *M. inpa* KENSLEY & WALKER. Studies of the larval development of these species would certainly be useful not only for taxonomic purposes but also for ecological and population studies. The aim of this paper is to describe the morphology of the three larval and first juvenile stages of *Macrobrachium nattereri,* to provide illustrations of the most important structures, and to compare them with those of the other known South American *Macrobrachium* species with abbreviated larval development.

Material and Methods

In July, 1983 a single berried female of *Macrobrachium nattereri* was collected in a small terra-firme, forest stream in a forest reserve (Reserva Florestal Ducke) near Manaus. Transportation of the female, its maintenance in the laboratory, rearing of the larvae, dissection and preparation of the larvae for illustration and measuring follow the procedures explained in MAGALHÃES (1988), except for the fact that food was not offered before metamorphosis. For greater clarity, plumose setae are shown as simple naked setae in the drawings of the whole animal.

Results

M. nattereri goes through three, benthic, larval stages. The larvae do not feed, but survive until metamorphosis by utilizing their rich yolk supply. The duration of each larval stage was not measured, but the larval period seems to last about one week, since the time between the hatching of the first larva and the metamorphosis of the last did not exceed 8 days.

Description of the larval stages and juvenile I

Body

L a r v a I (Total length 4.98 mm; n = 1) (Figs. 1, 2): Rostrum short, unarmed, strongly curved downwards. Carapace smooth. Eyes sessile. Abdomen smooth, the segmentation between the 6th abdominal somite and telson not very distinct; ventral borders of pleurae incomplete.

L a r v a II (Total length 5.19 mm; n = 1) (Figs. 16, 17): Rostrum slightly curved downwards, reaching distal end of the antennular peduncle; upper border with 5 minute teeth, lower border unarmed. Carapace with 2 minute spines on the antero-lateral border. Eyes stalked. Abdomen with ventral borders of the pleura distinct.

L a r v a III (Mean total length 5.69 mm; n = 3) (Figs. 29, 30): Rostrum with upper border bearing 8 small teeth and some short plumose setae; lower border with 1 minute tooth and glabrous.

J u v e n i l e I (Mean total length 6.40 mm; n = 3) (Figs. 41, 42): Rostral formula 8 - 9/ 1 - 2; short plumose setae also on the lower border.

Antennule

L a r v a I (Fig. 3): Peduncle unsegmented, but some joints visible under the cuticle. Distal flagella partially fused; inner flagellum tipped with a short weakly plumose seta, outer flagellum longer than the inner one and tipped with 3 minute naked setae.

L a r v a II (Fig. 18): Peduncle 3-segmented, bearing several naked and plumose setae as illustrated. Proximal segment with a ventral spine, a distal spine on the outer corner and a rounded stylocerite bearing 3 minute naked setae. Distal segment with 2 naked setae on the antennular lobe. Inner flagellum indistinctly 6-articulated, tipped with a minute naked seta. Outer flagellum subdivided after the first basal segment; outer branch longer than the inner one, which is tipped with 4 aesthestes.

L a r v a III (Fig. 31): Peduncle with an increased number of setae, including 10 plumose setae marginally and dorsally on the stylocerite, and a row of very small naked setae in the region of the developing statocyst. Inner flagellun distinctly 6-articulated. Outer flagellum with outer branch longer, 6-articulated; inner flagellun distinctly 6-articulated; inner branch tipped with 2 aesthetes. Both flagella bearing small setae, but minute aesthetes present only on the inner one.

J u v e n i l e I (Fig. 43): Peduncle more setose. Stylocerite sharp. Inner flagellun 9-articulated. Outer flagellum with a 10-articulated outer branch and a 2-articulated inner branch, which bears 2 distal and 1 subdistal aesthetes.

Antenna

L a r v a I (Fig. 4): Protopod not clearly segmented. Scale unsegmented, narrow, with 11 plumose setae along inner and distal margins and 3 rudimental setae on the inner margin. Endopod as an unsegmented flagellum, about twice as long as the scale.

Larva II (Fig. 19): Protopod bisegmented. Scale with a spine on the disto-lateral corner, 10 plumose setae and some rudimentary setae along the distal and inner margins. Endopod about 2.8 times as long as the scale, multi-articulated, although the proximal articles are only faintly divided.

Larva III (Fig. 32) and Juvenile I: Basis with a ventral spine. Scale with several plumose setae along distal and inner margins. Endopod multi-articulated, about 3.5 and 5 times as long as the scale, respectively, in larva III and juvenile I.

Mandibles

Larvae I (Fig. 5), II (Fig. 20) and III (Fig. 33): Rudimentary. Left and right mandibles alike. Cleft between incisor and molar processes increasing from first to third larval stages.

Juvenile I (Fig. 44): Fully developed, strong. Incisor process with 3 teeth; molar process stouter, with rounded and sharp teeth and several denticles.

Maxillula

Larvae I (Fig. 6), II (Fig. 21) and III: Rudimentary. Coxal and basal endites with some distal and subdistal protuberances. Endopod smooth and simple in the first stage, bilobed and bearing a minute spine on the lower lobe in the others.

Juvenile I (Fig. 45): Fully developed. Coxal and basal endites with several, naked and weakly plumose, setae terminally and subterminally. Lower lobe of endopod with a spine.

Maxilla

Larvae I (Fig. 7), II and III: Protopod rudimentary. Endopod with a rudimentary spine in the first stage, smooth in the others. Scaphognathite large, fringed by several plumose setae.

Juvenile I (Fig. 46): Protopod with 6 naked setae on both lower and upper border. Endopod with 3 weakly plumose setae proximally on the outer border.

Maxilliped 1

Larva I (Fig. 8): Protopod with a bilobed epipod and the inner margin slightly bilobed, smooth. Endopod short and smooth. Exopod long, with 3 terminal plumose setae and a rudimentary seta; proximal outer border slightly bulged and bearing 3 plumose setae.

Larva II (Fig. 22): Protopod with a trilobed epipod. Exopod with 4 terminal plumose setae; proximal outer margin more bulged, bearing 8 plumose setae.

Larva III (Fig. 34): Protopod distinctly bilobed, basal endite with a weakly plumose setae, coxal endite with a rudimentary seta. Exopod with 9 plumose setae on its proximal outer border.

Juvenile I (Fig. 47): Fully developed. Basal and coxal endites respectively with 7 and 30, naked and weakly plumose setae terminal and subterminal. Endopod with 1 subterminal weakly plumose seta.

Maxilliped 2

Larva I (Fig. 9): Protopod bisegmented, smooth. Endopod 4-segmented, although some joints are faint; last segment with 3 naked setae and a long, incurved terminal spine. Exopod with 5 plumose setae.

Larva II (Fig. 23): Coxa with a slightly bilobed epipod. Endopod with the terminal spine much reduced.

Larva III (Fig. 35): Endopod distinctly incurved, 5-segmented; last segment subtriangular, with some rudimentary setae and 2 naked setae.

Juvenile I (Fig. 48): Fully developed. Coxa with 3 naked setae on the inner margin and a large bilobed epipod. Endopod with antepenultimate segment bearing 1 naked seta; penultimate bearing 5 weakly plumose setae on the outer margin and 4 naked setae on distal margin; last segment with several, naked and weakly plumose setae terminally and subterminally.

Maxilliped 3

Larvae I (Fig. 10) and II: Protopod bisegmented. Endopod 4-segmented, although the joints are faint in the first stage. Last segment of endopod with 2 naked setae and a terminal spine, which is larger in the larva I. Exopod with 6 plumose setae.

Larva III: Coxa with an epipod. Endopod with 1, 2, 6, 2, naked and weakly plumose setae from proximal to distal segment.

Juvenile I (Fig. 49): Coxa and basis with 2 and 3 naked setae, respectively. Endopod 3-segmented, bearing several naked and weakly plumose setae situated mainly on the inner margin of the segments; terminal spine much reduced. Exopod shorter than in the larval stages.

Pereiopods 1 and 2

Larva I (Figs. 11, 12): Well developed, uniramous, chelate buds; joints indistinct. Pereiopod 2 larger than pereiopod 1.

Larva II (Figs. 24, 25): All joints distinct; a few rudimentary setae present.

Larva III (Figs. 36, 37): Some naked setae scattered from coxa to dactyl. Pereiopod 1 with inner margin of the carpus and palm with 4 and 2 spiniform plumose setae, respectively.

Juvenile I (Figs. 50, 51): Fully developed and functional. Setation increases, and tufts are present at the tip of the fixed and movable fingers.

Pereiopods 3, 4 and 5

Larva I (Fig. 13): All present as well developed, uniramous buds; joints indistinct.

Larvae II (Fig. 26), III (Fig. 38) and Juvenile I (Fig. 52): All functional. Protopod bisegmented. Endopod 5-segmented, with a short terminal spine. Setation increases from larva II to juvenile I.

Pleopods 1 to 5

Larva I (Fig. 14a - e): Biramous, smooth buds.

Larva II (Fig. 27a - e): Both endopod and exopod with rudimentary setae. Endopod of pleopods 2 - 5 with developing appendices internae.

Larva III (Fig. 39a - c): Several marginal plumose setae present on the endopod (except for that of pleopod 1) and the exopod of all pleopods. Each appendix interna bears minute hooks.

Juvenile I (Fig. 53a, b): Protopod of pleopod 5 with 3 plumose setae. Endopod of pleopod 1 with 2 plumose setae. Exopod of pleopods 1 - 5 with 1 subterminal naked seta.

Uropod

Larva I (Fig. 15): Buds visible through the cuticle of the telson.

Larva II (Fig. 28): Posterior projection of protopod free, overreaching dorsally the proximal lateral margin of telson. Endopodal buds visible as small rounded lobes under the telson. Exopodal buds partially produced outwards, causing a distinct discontinuity on the lateral margin of the telson.

Larva III (Fig. 40): Totally free and functional. Protopod with 1 naked seta. Endopod with 19 - 20 marginal plumose setae, 5 short weakly plumose setae on the outer proximal border and several others dorsally. Exopod with 24 - 25 plumose setae along most of the inner and distal borders, and a few naked and plumose setae dorsally, ventrally and on the proximal outer border; outer distal corner with a fixed and stout, articulated spine.

Juvenile I (Fig. 54): Protopod with 3 naked setae. Setation of both endopod and exopod increased.

Telson

Larva I (Fig. 15): Fan-like; posterior margin broadly convex with 7 + 7 plumose setae and a pair of minute naked setae (these setae are placed in a very faint median notch).

Larva II (Fig. 28): Lateral margin clearly bulged due to the position of the exopodal buds of the uropods. Posterior margin with 6 + 6 plumose setae and a pair of lateral spines.

Larva III (Fig. 40): Narrower and longer than in the preceding stage; wider and with 2 median dorsal, naked, spines anteriorly. Posterior part with a pair of dorso-lateral spines. Postero-lateral margins with 2 pairs of spines. Disto-lateral corners with a large spine. Posterior margin slightly convex, bearing 4 plumose setae.

Juvenile I (Fig. 54): A little narrower posteriorly, with 2 pairs of dorso-lateral spines, the proximal pair placed more dorsally. Disto-lateral corners bearing 2 pairs of spines, the inner one the largest. Posterior margin narrow and convex, with a small median point, and bearing 4 subterminal plumose setae ventrally.

Color of the larvae

In an overall view, the larvae are reddish and this is due to the rich red yolk supply and to the abundant distribution of red dendritic chromatophores. Under a low power microscope, these chromatophores are seen on the eyes and ocular peduncles, the antennular peduncles, the bases of the antennas, the anterior region of the carapace, the dorso-lateral region of the abdominal somites, the telson near the anus and near the posterior margin. Ventrally, chromatophores are present on the buccal region, the bases of the maxillipeds and pereiopods 1 to 3, between the bases of the 2nd, 3rd and 4th pereiopods and between the 3rd and 4th pleopods. Dark chromatophores are also present on the eye and anteriorly on the dorso-lateral region of the carapace.

Discussion

As only one ovigerous female of *M. nattereri* was available and, thus, a small number of larvae could be studied, we could obtain only a restricted number of life history data for this species. Although the exact duration of each larval stage was not determined, the whole larval period did not exceed 8 days. Brief larval periods, usually no longer than 7 days, seem to be common for palaemonid shrimps with abbreviated development: *M. asperulum* (VON MARTENS) takes less than 3 days to reach metamorphosis (SHOKITA 1977), *M. brasiliense* needs 7 - 11 days (VEGA unpubl.), *M. pilimanus* (DE MAN) 5 days (CHONG & KHOO 1987b), *Palaemonetes paludosus* (GIBBES) 5 - 10 days (DOBKIN 1963), *P. ivonicus* HOLTHUIS 4 - 6 days (MAGALHÃES 1986) and *Pseudopalaemon chryseus* KENSLEY & WALKER 5 - 7 days (MAGALHÃES 1986/87), to cite a few examples. In our material, the number of eggs per female and the measurements of fresh eggs were not determined. However, the females of *M. nattereri* carry relatively few and large eggs. According to RODRÍGUEZ (1982), females of this species carry 34 to 150 eggs, measuring 2.14 - 2.58 mm in diameter.

As already mentioned, *M. nattereri* and *M. brasiliense* are closely related. They both occur in the Amazon basin and, in many cases, even adult specimens are not easily identified. Although their larval development is similar in many respects, some differences can be mentioned: (1) The first larval stage. In *M. nattereri,* the endopod of the antenna, maxillipeds 2 and 3, and the pereiopods are unsegmented or the segmentations are indistinct, while in *M. brasiliense* these segmentations are clearly visible. *M. nattereri* does not bear appendices internae on pleopods 2 - 4, while *M. brasiliense* does. In *M. brasiliense,* the 6th abdominal somite is separated, while in *M. nattereri*, this separation is indistinct. Both species have 7 + 7 plumose setae on the posterior margin of the telson, but in *M. brasiliense* this margin is clearly bilobed due to a distinct bulging of the disto-lateral corners and a deep median notch. In *M. nattereri*, this margin is broadly convex, showing only a faint median notch. (2) The second larval stage. Here, the antennal scale of *M. nattereri* has a few plumose setae only on part of its distal and inner margins, while *M. brasiliense* has more numerous setae along these margins. The pleopods of *M. nattereri* show only rudiments of setae, but in *M. brasiliense* the endopod of the pleopods already bear plumose setae. (3) The third

larval stage. *M. nattereri* shows several structures in a more rudimentary state than the corresponding ones in *M. brasiliense*, particularly the setation of the antennule, the maxillula, the protopodal endites of the maxilla, the inner margin of the protopod of maxilliped 1, the pereiopods and the pleopods. (4) The first juvenile. Here, the structures of both species are similar, except for the telson. In *M. nattereri*, the telson has 2 spines on the disto-lateral corner, and the posterior margin bears a small median point and four median plumose setae, while in *M. brasiliense* the posterior margin is rounded and bears 5 large spines and no plumose setae.

The above comparisions must be taken with some reserve, however, since the specimens of *M. brasiliense* studied by VEGA (unpubl.) came from Paraná State, Southeast Brazil (Rio Paraná basin). It would be interesting to know how similar the larval development of the Central Amazonian population of *M. brasiliense* is to that studied by VEGA.

The larval development of *M. nattereri* is also similar to that of *M. potiuna* and *M. iheringi*. However, in *M. potiuna* larva I has a long, multi-articulated antennal flagellum, larva III has the endopod of the uropods rudimentary, and the larva I to III have a greater number of plumose setae on the posterior margin of the telson (29 to 35). In addition, the shape of the telson is also different in these larvae. Most of the structures of the larvae of *M. iheringi* closely resemble the corresponding one in *M. nattereri*. The former species differs by showing rudimentary exopods on pereiopods 1 to 4 and by the shape of the telson which, in the second larval stage, shows no bulged lateral margins.

M. ferreirai also has an abbreviated development with three larval stages (MAGALHÃES & WALKER 1988). Larval development of *M. inpa* has not been studied yet, but this species probably has abbreviated development due to the fact that the eggs are few and large (6 - 30 eggs/female; mean egg size of 1.76 x 1.31 mm, data from WALKER & FERREIRA 1985) and also because it inhabits the mineral- and plankton-poor waters of the Central Amazonian terra-firme forest streams. In such habitates, only species showing abbreviated or extremely abbreviated development have been found (MAGALHÃES & WALKER 1988).

Resumo

O desenvolvimento larval em cativeiro do camarão dulcícola *Macrobrachium nattereri* (HELLER) foi estudado a partir da prole de uma fêmea ovada coletada em um pequeno igarapé de floresta de terra-firme próximo a Manaus. O desenvolvimento foi abreviado, com 3 estágios larvais. As larvas, bentônicas e ricas em vitelo, não ingeriram alimento até a metamorfose. A larva recém-eclodida apresentou olhos sésseis e todos os apêndices, com a exceção dos urópodos; entretanto, a maioria dos apêndices não estavam totalmente formados. O período larval não excedeu 8 dias. São fornecidas descrições e ilustrações dos 3 estágios larvais e do primeiro estágio de juvenil e são feitas comparações com as larvas de outros *Macrobrachium* sul-americanos com desenvolvimento larval abreviado conhecido.

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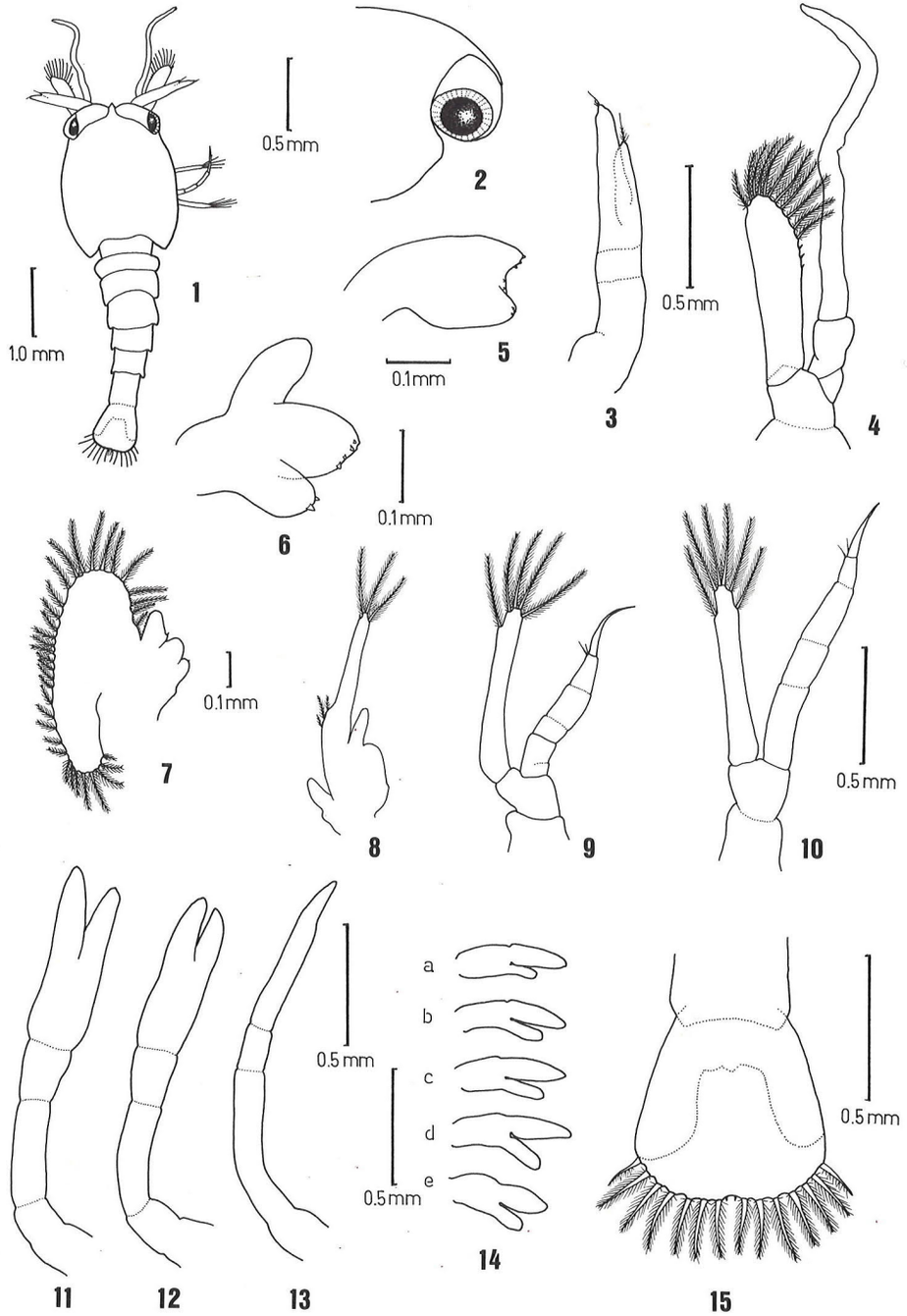
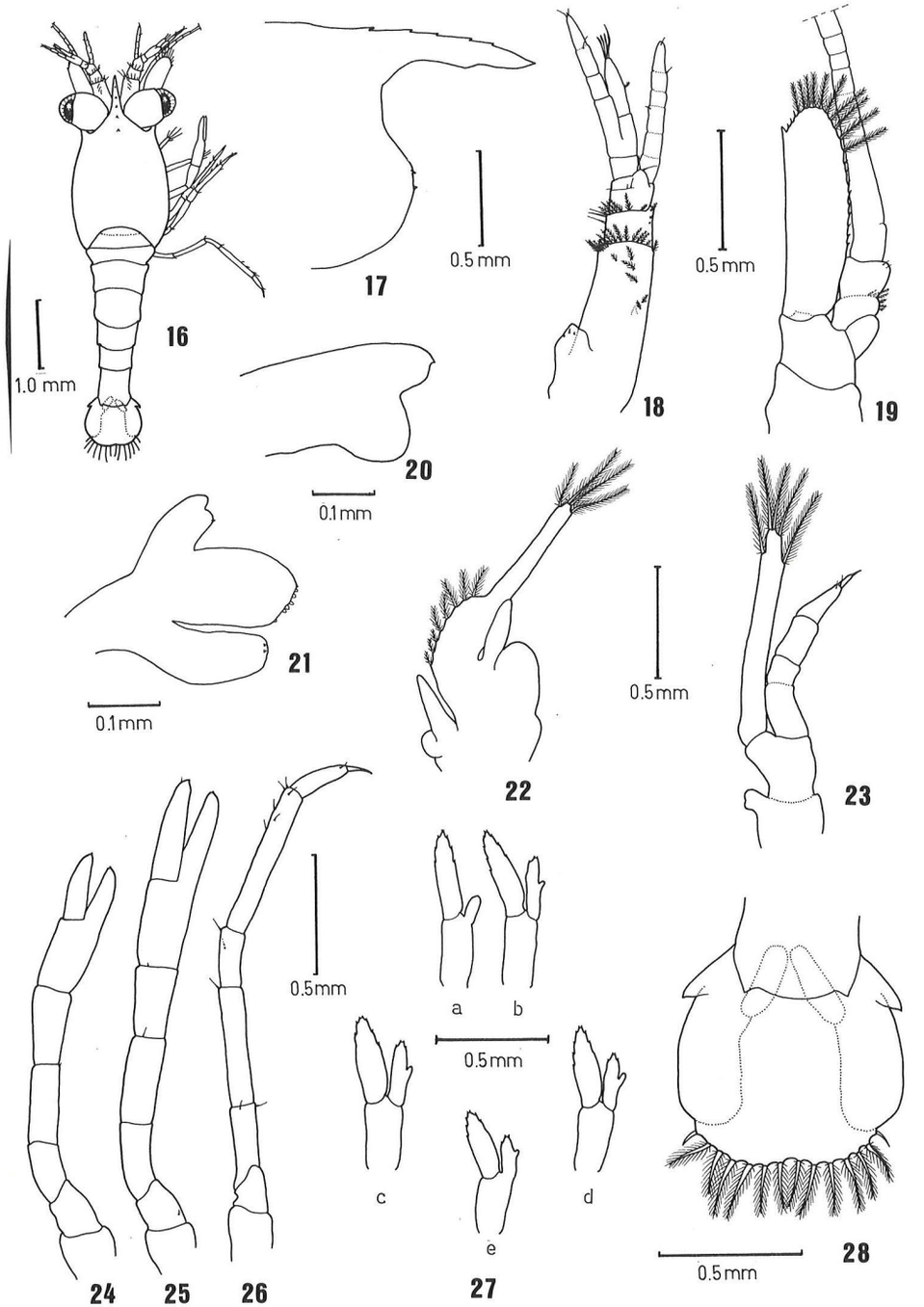
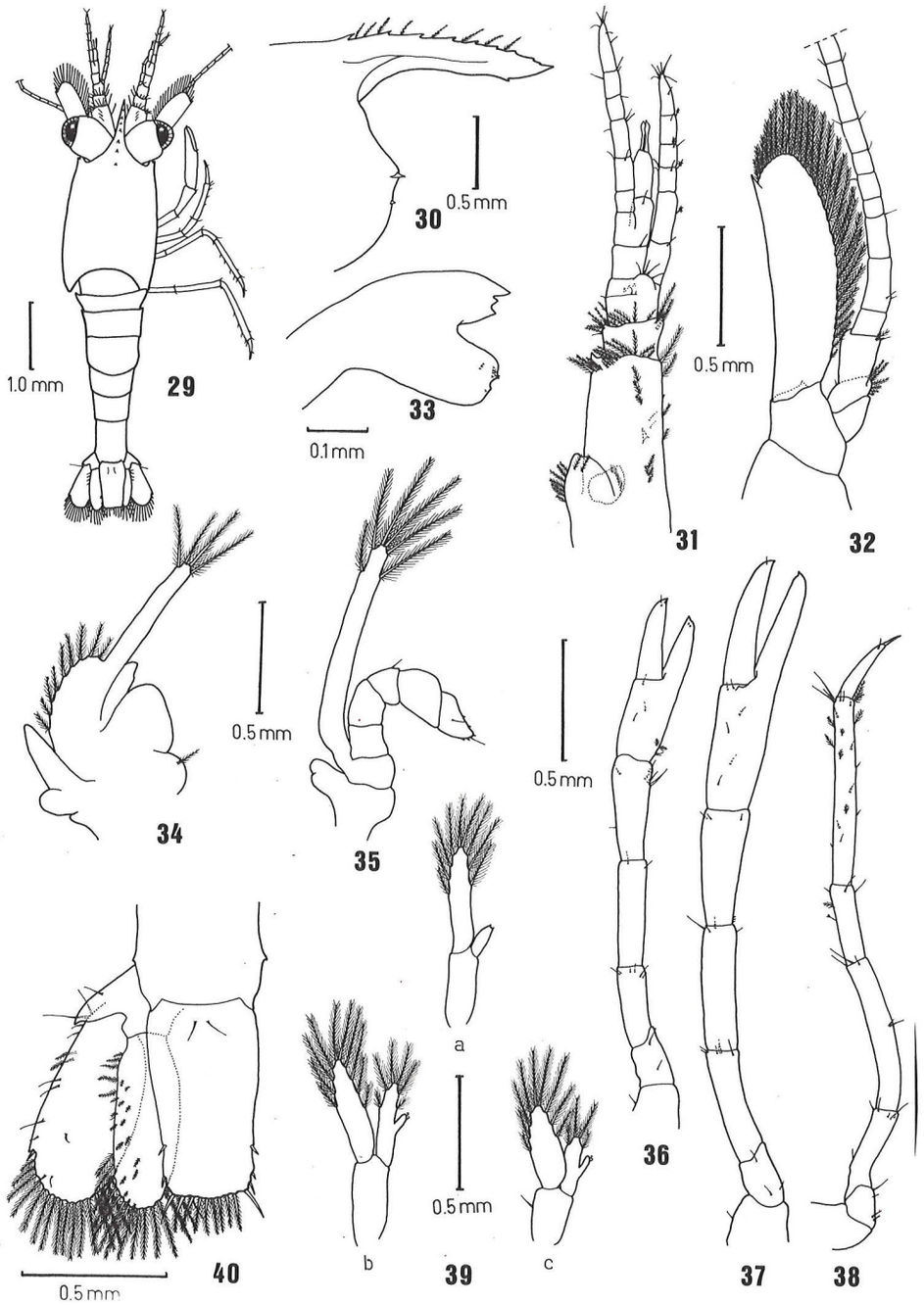


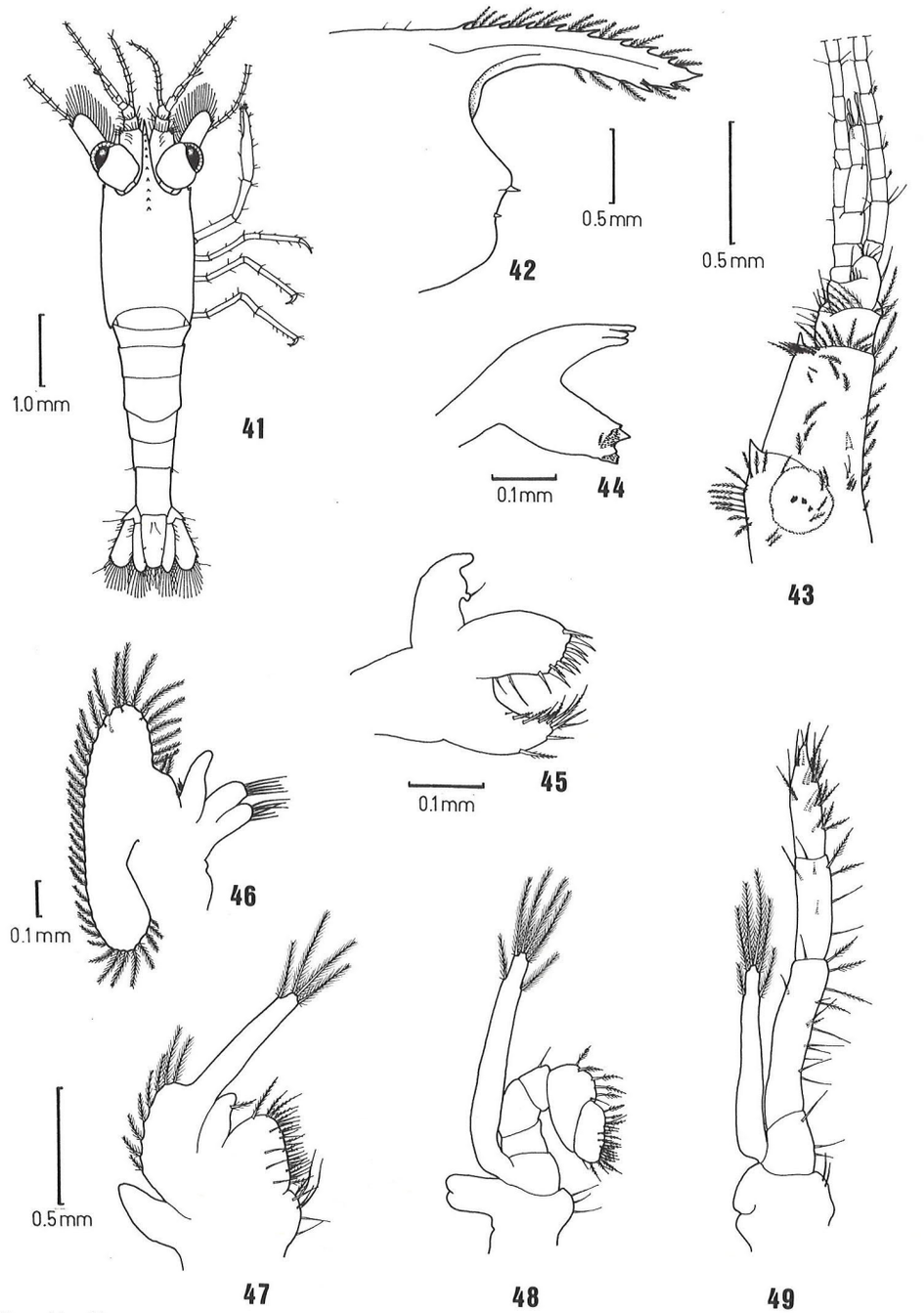
Figs. 1 - 15:
Macrobrachium nattereri, larva I:
1: Dorsal view; **2:** Lateral view of the anterior region of the carapace; **3:** Antennule; **4:** Antenna; **5:** Left mandible; **6:** Maxillula; **7:** Maxilla; **8:** Maxilliped 1; **9:** Maxilliped 2; **10:** Maxilliped 3; **11:** Pereiopod 1; **12:** Pereiopod 2; **13:** Pereiopod 5; **14a - e:** Pleopods 1 to 5; **15:** Telson.



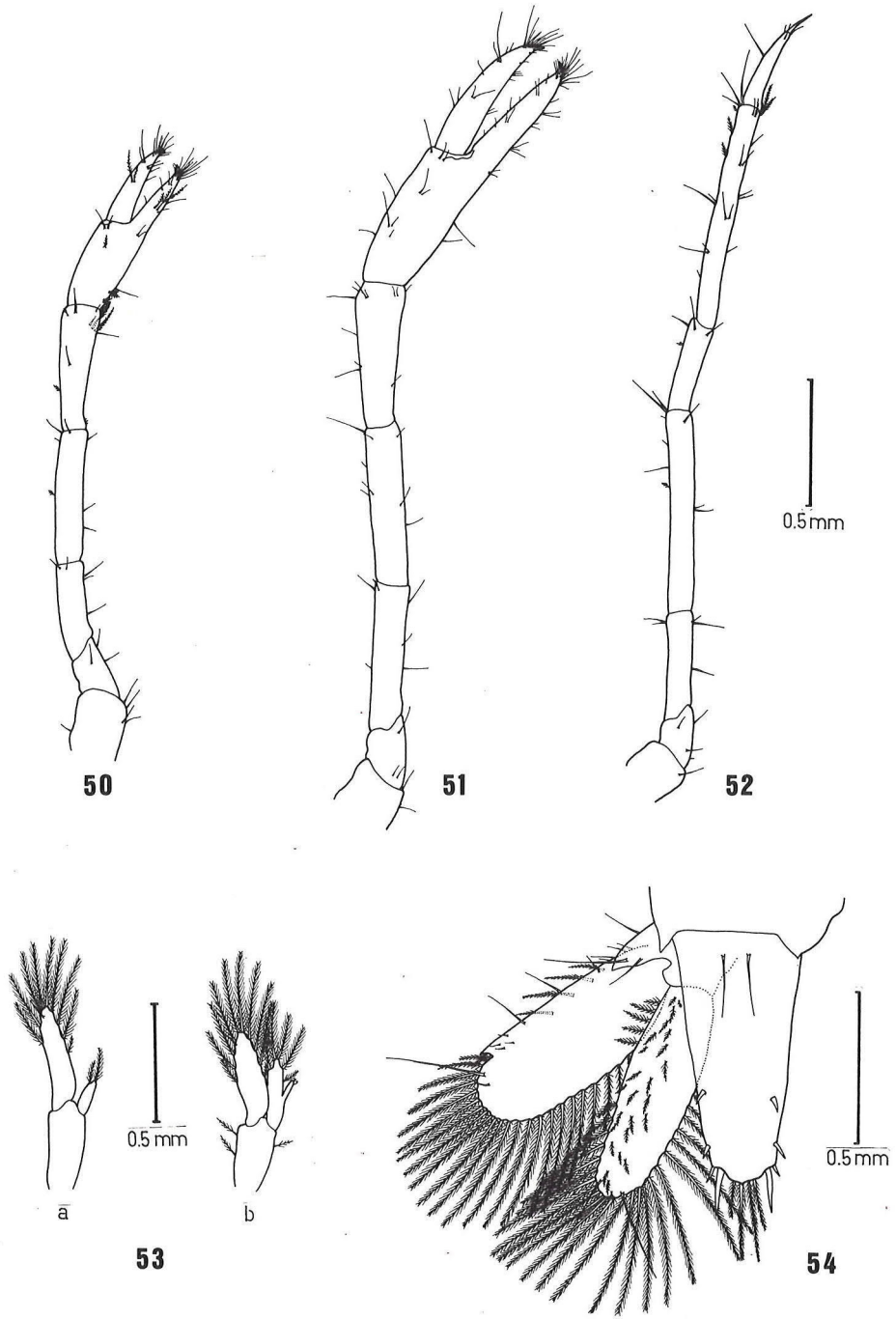
Figs. 16 - 28:
Macrobrachium nattereri, larva II:
16: Dorsal view; **17:** Lateral view of the anterior region of the carapace; **18:** Antennule; **19:** Antenna; **20:** Left mandible; **21:** Maxillula; **22:** Maxilliped 1; **23:** Maxilliped 2; **24:** Pereiopod 1; **25:** Pereiopod 2; **26:** Pereiopod 5; **27a - e:** Pleopods 1 to 5; **28:** Telson.



Figs. 29 - 40:
Macrobrachium nattereri, larva III:
29: Dorsal view; **30:** Lateral view of the anterior region of the carapace; **31:** Antenulle; **32:** Antenna; **33:** Left mandible; **34:** Maxilliped 1; **35:** Maxilliped 2; **36:** Pereiopod 1; **37:** Pereiopod 2; **38:** Pereiopod 5; **39a - c:** Pleopods 1, 2 and 5; **40:** Left uropod and telson.



Figs. 41 - 49:
Macrobrachium nattereri, juvenile I:
41: Dorsal view; **42:** Lateral view of the anterior region of the carapace; **43:** Antennule; **44:** Left mandible; **45:** Maxillula; **46:** Maxilla; **47:** Maxilliped 1; **48:** Maxilliped 2; **49:** Maxilliped 3.



Figs. 50 - 54:
Macrobrachium nattereri, juvenile I:
50: Pereiopod 1; **51:** Pereiopod 2; **52:** Pereiopod 5; **53a, b:** Pleopods 1 and 5; **54:** Left uropod and telson.